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THE MAMMALIAN FAUNA OF MADURA CAVE, WESTERN AUSTRALIA PART V: DIPROTODONTA (PART)

ERNEST L. LUNDELIUS, JR.

WILLIAM D. TURNBULL

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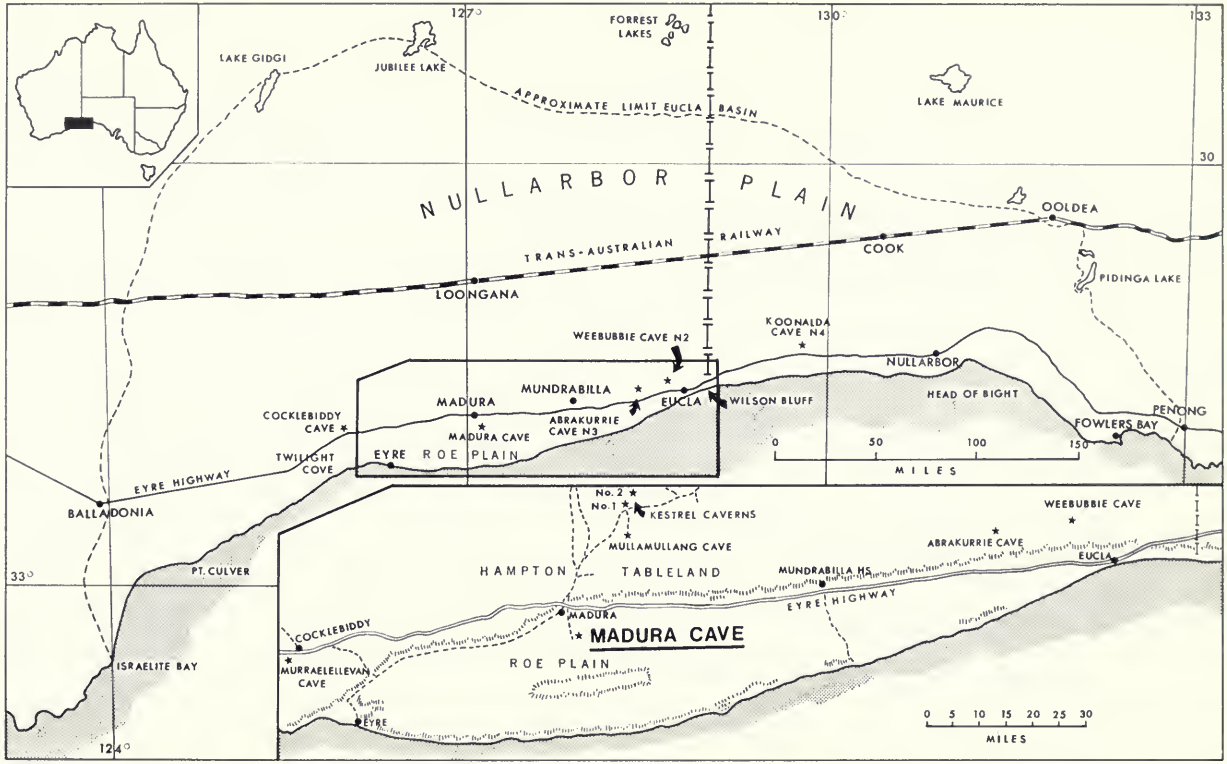

FRONTISPIECE. Maps of the Nullarbor Plain area showing Madura Cave on the Roe Plain to seaward of the Hampton Scarp. Also shown are some other nearby caves on the Hampton Tableland, above the scarp.

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CONTENTS

List of Illustrations vi
List of Plates (SEM Photos) vi
List of Tables vii
Abstract 1
Introduction 1
Systematics 2
Lasiorhinus (Gray, 1863) 2
Lasiorhinus c.f. *latifrons* (Owen, 1845) 2
Material 2
Description 2
Discussion 12
Vombatidae 12
Genus and species indeterminate 12
Material 12
Phascolarctos Blainville, 1816 13
Phascolarctos cinereus (Goldfuss, 1817) 13
Material 13
Description 13
Discussion 15
Trichosurus Lesson, 1828 18
Trichosurus vulpecula (Kerr, 1792) 18
Material 18
Description 18
Pseudocheirus Ogilby, 1837 20
Pseudocheirus peregrinus (Boddaert, 1785) 20
Material 20
Description 20
Discussion 20
Cercartetus Gloger, 1841 22
Cercartetus concinnus (Gould, 1845) 22
Material 22
Description 23
Discussion 29
Summary 30
Acknowledgments 30
Literature Cited 31

LIST OF ILLUSTRATIONS

Figures

FRONTISPIECE: Maps of the Nullarbor Plain area ii
1. *Lasiorhinus* c.f. *latifrons*, right I_1 3
2. *Lasiorhinus* c.f. *latifrons*, maxillary fragment 5
3. *Lasiorhinus* c.f. *latifrons*, anterior moiety of an upper molar 6
4. *Lasiorhinus* c.f. *latifrons*, upper molar 7
5. *Lasiorhinus* c.f. *latifrons*, molar tooth 8
6. Vombatidae gen. and sp. indet., half of one moiety of a molar tooth 9
7. *Phascolarctos cinereus*, right M^2 and left M_4 14
8. *Trichosurus vulpecula*, left M_1 19
9. *Pseudocheirus peregrinus*, right M^1 21
10. *Cercartetus concinnus*. Schematic outlines of 14 ramus fragments 24,25

Plates

I. *Lasiorhinus* c.f. *latifrons* 10
II. *Lasiorhinus* gen. and sp. indet. 11
III. Montages of *Phascolarctos cinereus* and of *Trichosurus vulpecula* and a stereopair of *Pseudocheirus peregrinus* 16,17
IV. *Cercartetus concinnus* 26,27

LIST OF TABLES

1. Measurements and ratios of upper dentitions of *Phascolarctos cinereus* 13
2. Measurements of lower dentitions of *Phascolarctos cinereus* 15
3. Measurements of *Trichosurus*, M_1 20
4. Measurements on fossil and Recent specimens of *Pseudocheirus peregrinus* 21

ABSTRACT

Five species of the Order Diprotodonta are reported from the deposits of Madura Cave.

The vombatid *Lasiorhinus* c.f. *latifrons* is represented by teeth from mostly juvenile individuals from Levels 2 through 4–5 in Trenches 1, 3, and 4. Some indeterminate juvenile specimens may represent another vombatid taxon. They are present throughout the excavated sequence (7,500–38,000 years B.P.). Several specimens are noteworthy for the preservation of some of the original tooth crown features.

Three teeth of *Phascolarctos cinereus* from a level in Trench 4 dated 20,000 y B.P. imply more mesic conditions than exist at present.

One tooth each of *Trichosurus vulpecula* and *Pseudocheirus peregrinus* was recovered from units dated 20,000 y B.P. and 15,600 y B.P., respectively. Today these taxa live in more humid environments than are found on the Nullarbor.

Sixteen mandibles and eight isolated teeth of *Cercartetus concinnus* came from the Pleistocene units (15,000–38,000 y B. P.), but none were found in Unit 1, the Holocene unit.

At present none of these taxa are found in the area of Madura Cave, although *Lasiorhinus latifrons* occurs in similar habitats in nearby South Australia and *Cercartetus concinnus* is found at the eastern and western edges of the Nullarbor Plain. *Phascolarctos cinereus*, *Pseudocheirus peregrinus*, and *Trichosurus vulpecula* are restricted to more mesic environments, and they occur only in the 15,000- to 20,000-y B.P. interval.

INTRODUCTION

This portion of the Madura Cave work continues the systematic section begun in Part I and continued in Parts II, III, and IV (Lundelius & Turnbull, 1973, 1975, 1978, 1981) and covers part of the Order Diprotodonta, specifically the Vombatidae (*Lasiorhinus* c.f. *latifrons*), Phascolarctidae (*Phascolarctos cinereus*), Phalangeridae (*Trichosurus vulpecula* and *Pseudocheirus peregrinus*), and Burramyidae (*Cercartetus concinnus*).

Measurements and abbreviations used are either those in standard use or they have been outlined in one of the previous sections. The Hershkovitz (1971) summary is used for alternative dental terminologies.

SYSTEMATICS (section continued)

CLASS MAMMALIA (continued)
Subclass Theria (continued)
Infraclass Eutheria (continued)
Cohort Marsupiata (*sensu* Turnbull, 1971; = Metatheria) (continued)
Order Diprotodonta (Owen, 1866; revised Ride, 1964; Kirsch, 1968)
Family Vombatidae
Lasiorhinus (Gray, 1863)

Lasiorhinus c.f. **latifrons** (Owen, 1845)

Material

Trench 1, 2½ ft level (about top of Unit 2)
PM 4782, left M_4 or right M^1 (fig. 5)

Trench 3, Unit 2, Level ?, probably Level 1
TMM 41106-71, right I_1
TMM 41106-72, right I_1 (fig. 1)

Trench 3, Unit 3, Level ?, probably Level 1
TMM 41106-52, fragment of the palatal portion of a left maxillary with symphysis and alveoli for posterior lobe of M^1 and for both lobes of M^2; associated with it are two teeth, one the posterior lobe of an M^1 that appears to fit the alveolus and a right M^1 at a very young age/wear stage (fig. 2; pl. I-A)

Trench 4, Unit 2, Level 1
PM 36833, half molar
PM 36834, half molar (fig. 3)
PM 36835, complete upper molar (fig. 4)
TMM 41106-5021, one lobe of a molar

Trench 4, Unit 2, Level 2
PM 36836, half a lobe of a molar, probably M_2, M_3, or M_4
PM 36838, half molar tooth

Trench 4, Units 4–5
TMM 41106-5022, an upper molar with one lobe heavily leached

Trench 5, Unit 6
WAM 75.1.142, nearly complete molar at an early wear stage (pl. I-B)
TMM 41106-5023, three quarters of a molar

Description

Most of the material from Madura Cave referred to *Lasiorhinus* c.f. *latifrons* represents juvenile individuals. Two relatively complete right I_1s show the characters stated by Merrilees (1967) to be diagnostic of that taxon (fig. 1). In cross section they are higher than wide, in contrast to *Vombatus hirsutus* in which the I_1s are wider than high. There is a stout enamel cover for the full length of the ventral (front) surface. This enamel band extends a short distance onto the medial and lateral sides of the tooth where it ends abruptly. The remainder of the tooth is covered by a thin layer of cementum that also extends over the enamel in places.

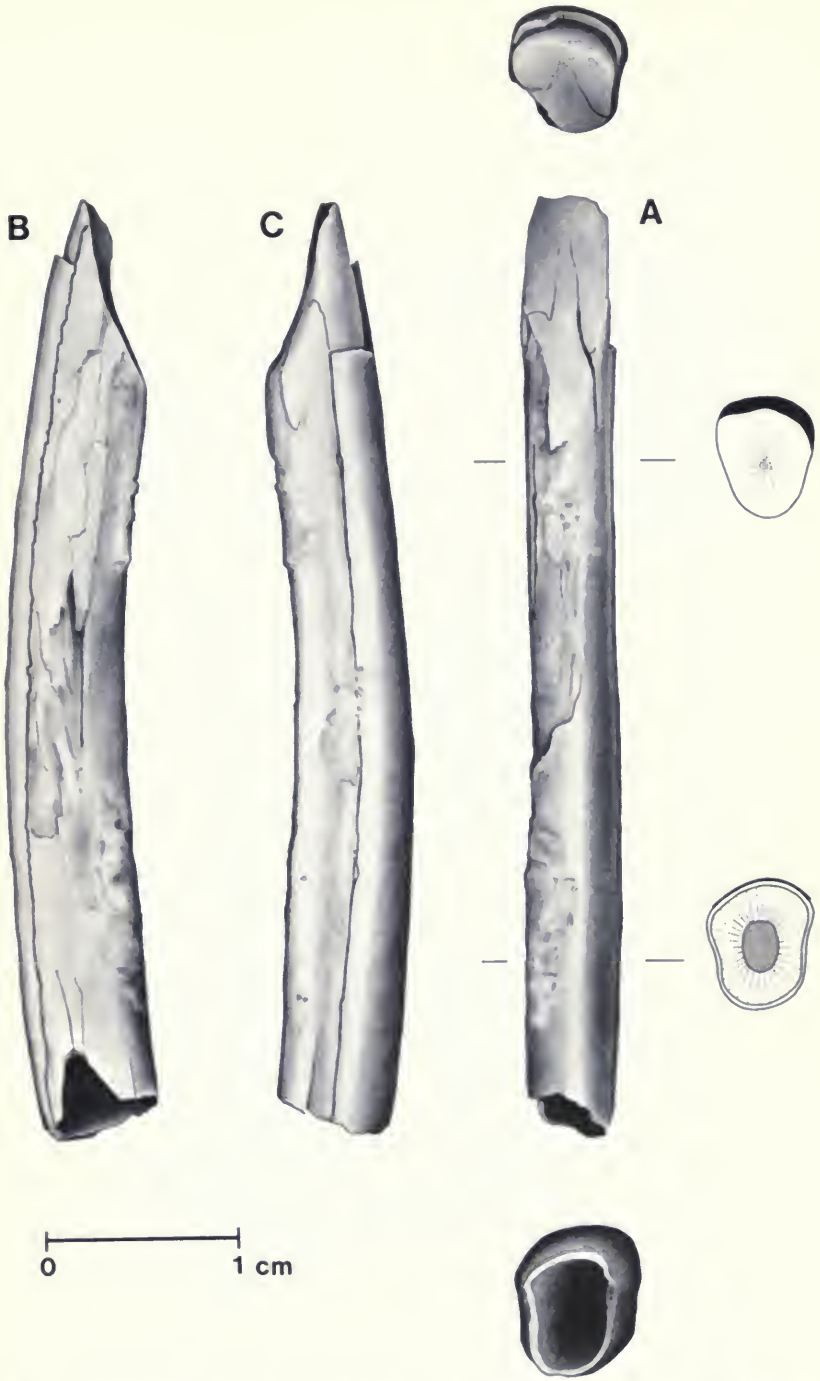


FIG. 1. *Lasiorhinus* c.f. *latifrons*, TMM 41106-72, a right I_1 shown in dorsal (occlusal) and crown and root **(A)**, mesial **(B)**, and distal **(C)** views. Two cross-sectional outlines are also given.

The wear surface is slightly concave anteroposteriorly and transversely, especially near the tip. It makes a more acute angle with the ventral surface of the tooth than is seen in *Vombatus*. This acute angle is also seen in a Recent specimen of *Lasiorhinus* (TMM M-943 A).

The palatal portion of the maxillary (TMM 41106-52), a fragment that extends from the midline to the alveolar border, shows the abrupt widening behind M^1 and parts of the alveoli for the posterior lobe of M^1 and both lobes of M^2 (fig. 2). Merrilees (1967) states that the least width of the palate between M^1 alveoli of opposite sides is wider in *Lasiorhinus* than in *Vombatus*. The Madura Cave specimen measures 3.5 mm from the posterior lobe of M^1 to the midline suture, which when doubled gives a total width of 7.0 mm. This is slightly narrower than any of Merrilees' specimens. Associated with the maxillary fragment in the matrix was one complete lobe of a molar whose shape and curvature fit the alveolus of the posterior lobe of M^1. It may or may not be part of the same individual as the maxillary fragment.

Isolated teeth of wombats are difficult to identify both as to taxon and as to position in the jaw, and in the case of molars, the difficulty even extends to whether they are upper or lower teeth. Merrilees (1967) has noted that the upper molars are usually more tightly curved, especially in *Lasiorhinus*, and that the anterior ones are more so than the posterior ones. He has also recognized the following criteria for distinguishing *Lasiorhinus* teeth from those of *Vombatus* in most cases: an inward (inflected) curvature of the enamel on the anterobuccal surface of the fore lobe of M_3 and M_4 of *Lasiorhinus* (it is also present on the M_2 of one of our comparative specimens, TMM M-943 B); the more rounded apices of the lobes of the molars in *Lasiorhinus*; and the more rounded aspect of the anterolabial and posterolabial corners of the upper molars and the anterolingual and posterolingual corners of the lower molars. All of the Madura Cave specimens assigned to *Lasiorhinus* showed strong development of one or more of these features. All post-incisor teeth in the Madura Cave collection that have been so assigned are molars, and no premolars have been recognized.

All the molars with sufficient wear and growth to have achieved the adult pattern show features typical of *Lasiorhinus*. They are open-rooted, bilobed, subtriangular prisms, with the apices of the lobes broadly rounded. The anterolingual and posterolingual (for lowers) and anterolabial and posterolabial (for uppers) corners of the teeth are smoothly rounded curves (figs. 3, 4), not more sharply angled as in *Vombatus*. Specimen PM 36834 (fig. 3) shows the inward curve (or concavity) of the enamel on one side of a lobe, and PM 36836 shows a concavity on both sides of the same lobe.

Enamel is absent from the lingual surfaces of the lower molars and the labial surfaces of the upper molars. A layer of cementum encases the tooth but is thickest in the "V" between the lobes and on those parts of the tooth that lack enamel. Where the enamel is absent the cement is in direct contact with the dentine and forms a distinct outer layer of the tooth of approximately the same thickness as the enamel. Often it mimics it closely. This is probably the reason for the statement in Stirton et al. (1967, p. 456) that "the enamel encircles the tooth." They referred to a premolar, but the condition is found to be common in all cheek teeth of all of our available specimens of modern *Vombatus hirsutus* and *L. latifrons*. Figure 5 shows one of the Madura Cave specimens that illustrates the condition very well, and Figure 6 shows the extent of the cementum.

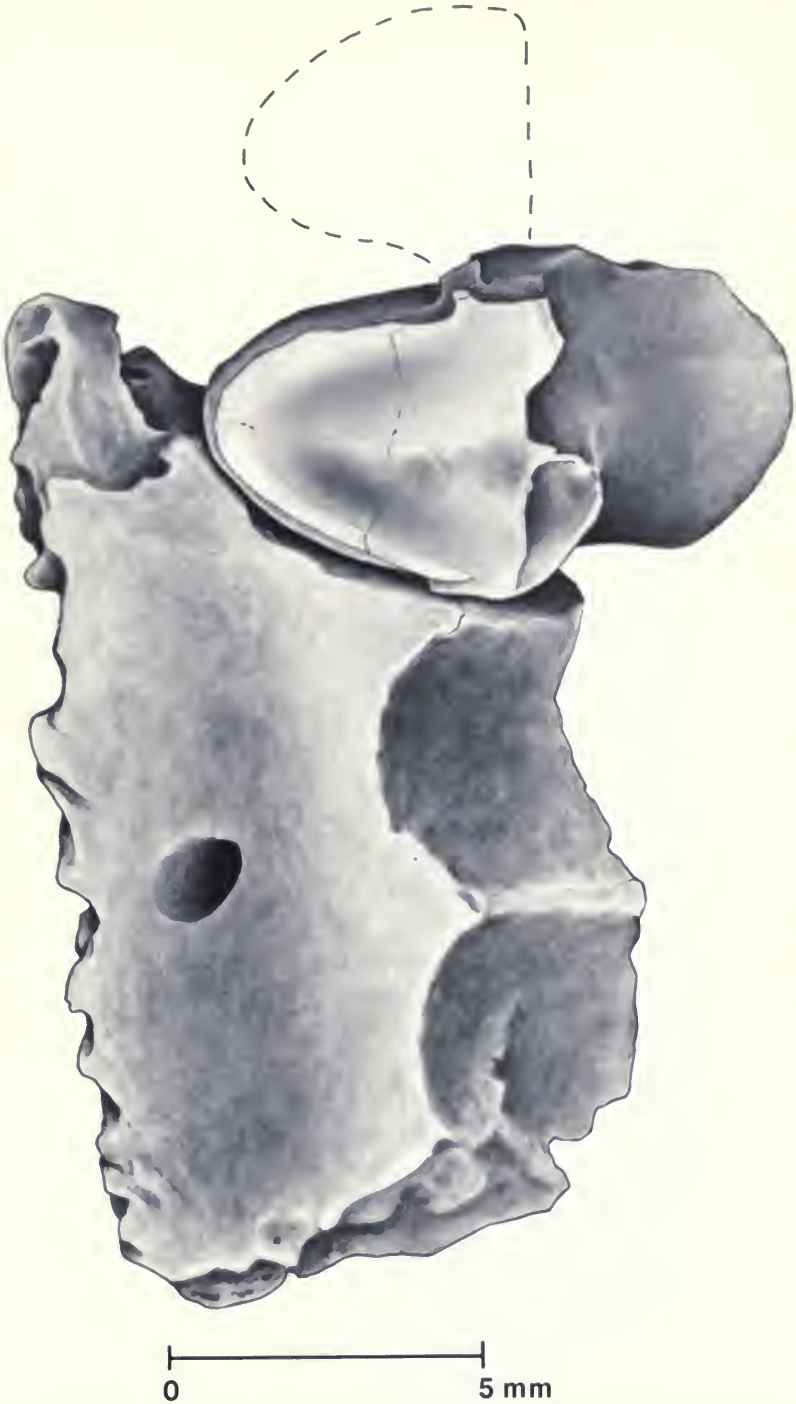


FIG. 2. *Lasiorhinus* c.f. *latifrons*, TMM 41106-52, a maxillary fragment shown in palatal view. The broken posterior tooth half was associated and appears to fit the posterior alveolus for the M_1.

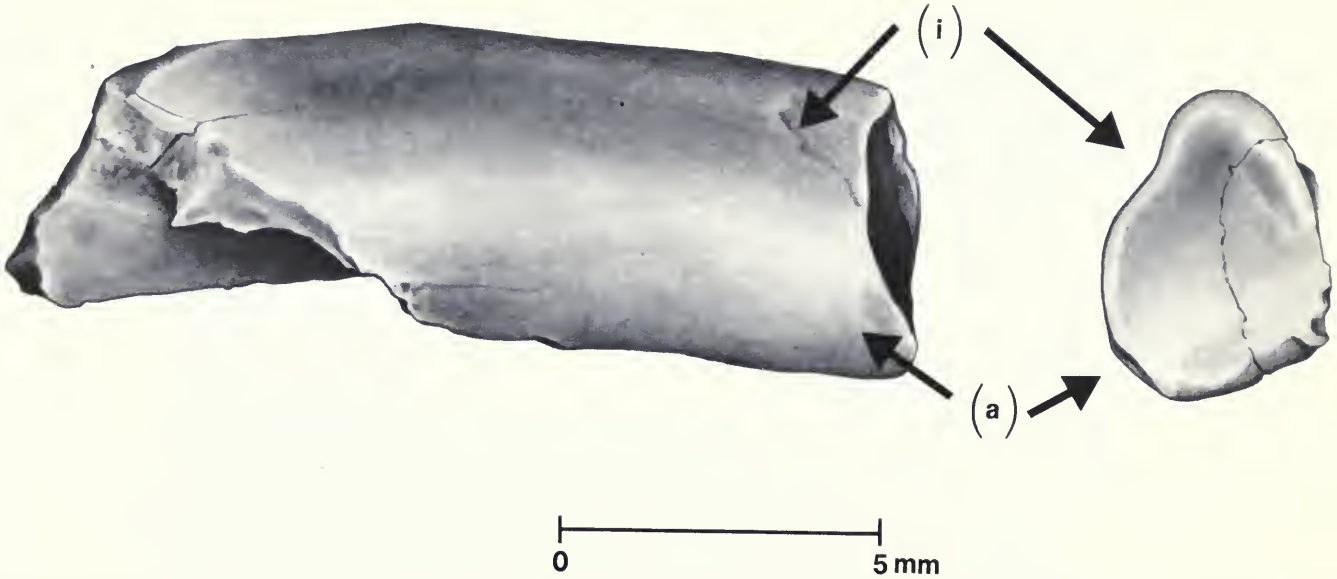


FIG. 3. *Lasiorhinus* c.f. *latifrons*, PM 36834, the anterior moiety of an upper molar showing the features of *Lasiorhinus* upper molars that are usually diagnostic (reported by Merrilees, 1967): **(i)** the inwardly inflected curve of the anterior side of the forelobe, **(a)** the gently rounded anterolabial and anterolingual corners. In *Vombatus* these corners (and those of the posterior lobe as well) tend to be sharper (more pointed) and there is no inflection to the anterior edge of the forelobe.

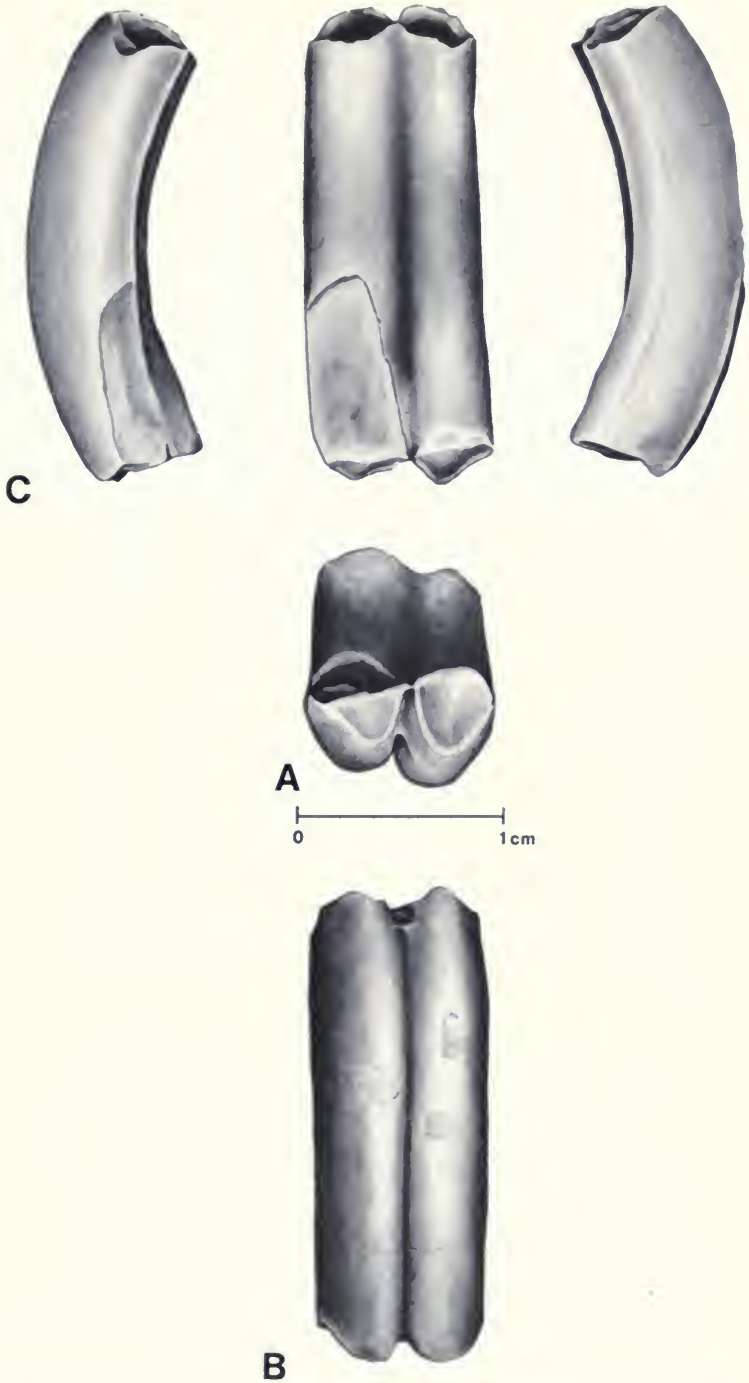


FIG. 4. *Lasiorhinus* c.f. *latifrons*, PM 36835, an upper molar shown in crown **(A)**; lingual **(B)**; and labial, mesial, and distal **(C)** views.

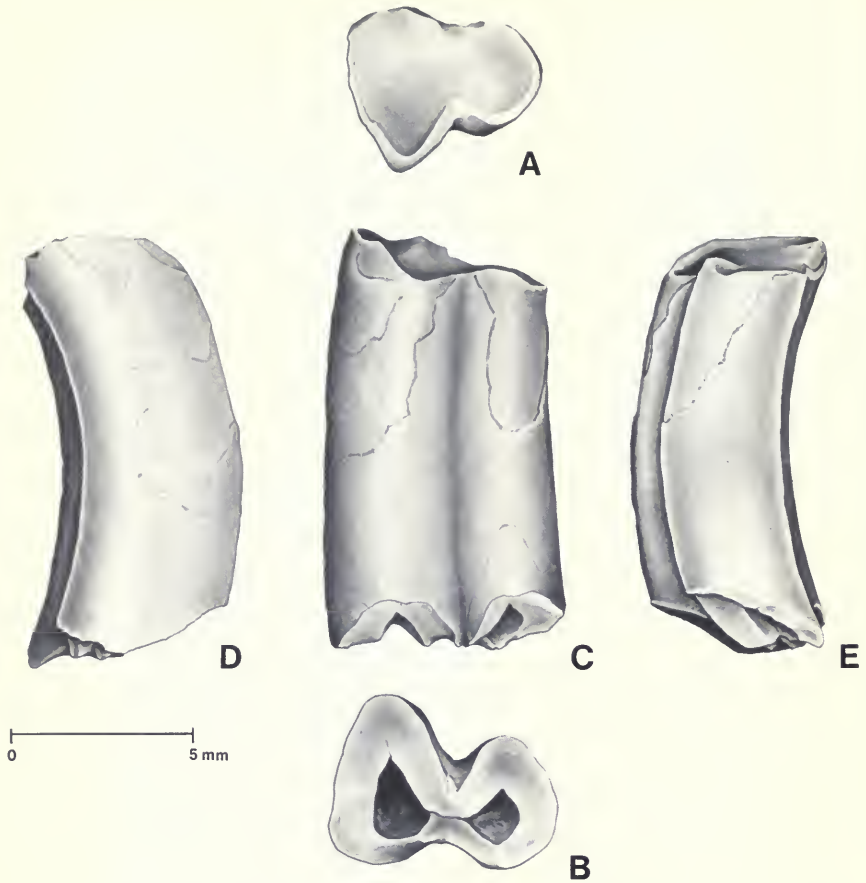


FIG. 5. *Lasiorhinus* c.f. *latifrons*, PM 4782, a molar tooth (either LM^4 or RM^1, or RM_1 or LM_4) shown in five views: crown **(A)**, root **(B)**, labial or lingual **(C)**, and proximal or distal **(D and E)**.

The worn occlusal surface of the tooth usually has low ridges, one on each lobe, that extend nearly transversely across the teeth almost to the apex of each lobe. On specimen WAM 75.1.142 (pl. I-B), which is from a very young individual, each of these low ridges originates at a shallow pit on the occlusal surface on the side of the tooth opposite the apices of the lobes. These pits appear to open into the pulp cavities and to be the sites of deposition of secondary dentine.

Three teeth, WAM 75.1.142 (pl. I-B), TMM 41106-52 (pl. I-A), and TMM 41106-5023, are from very young individuals. They show a distinct taper toward the crown. In TMM 41106-5023, which is one of the younger, the enamel partly covers the crown, and wear has produced one small oblique facet that is inclined toward the center of the tooth where the lobes coalesce. In one other tooth, TMM 41106-52, which is about at the same age/wear stage as TMM 41106-5023, the enamel has just gone from the crown, and some features of the

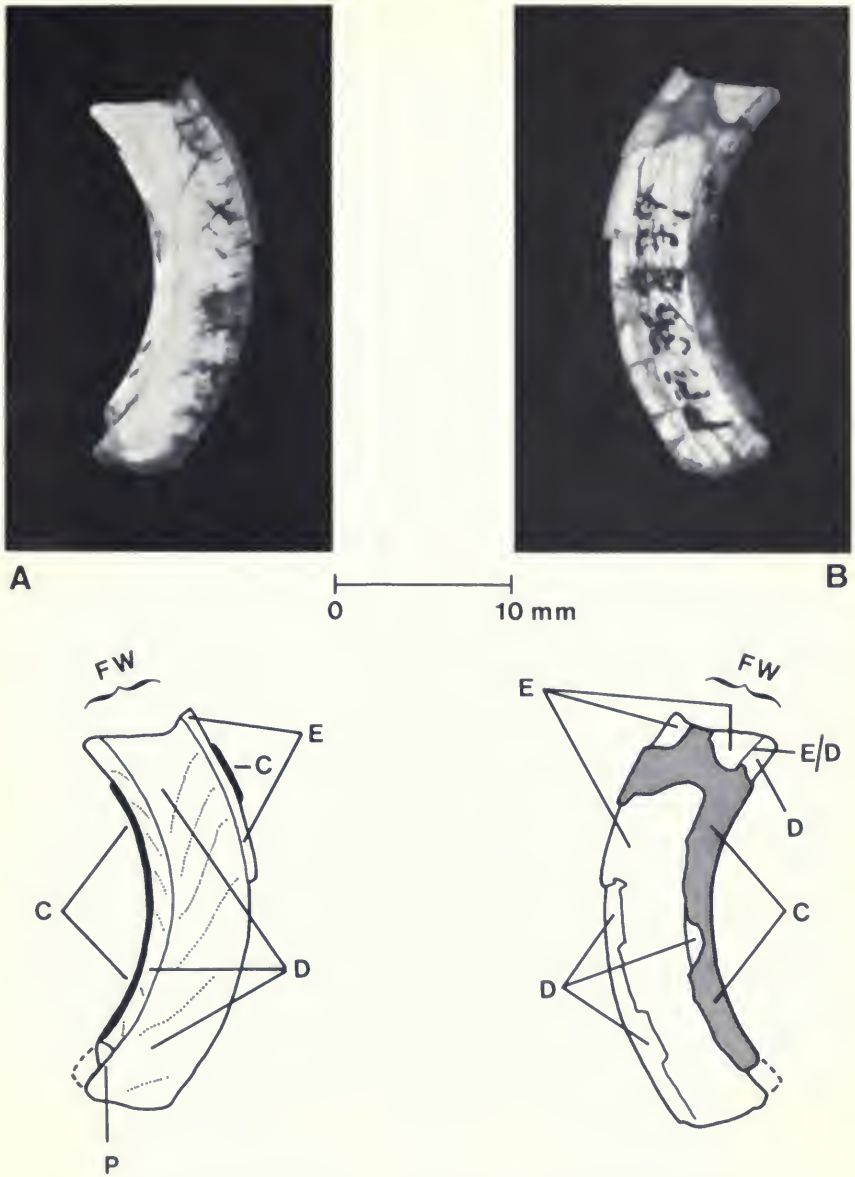


FIG. 6. Vombatidae gen. and sp. indet., PM 36837, one half of one moiety of a molar tooth preserving the external surface on one side and the now polished longitudinal section from near the center of the moiety on the reverse side. **A**, The section exposing the filled pulp canal **(P)**, the dentine **(D)**, the enamel which is seen along the convex curve **(E)**, and the superficial cementum covering **(C)** that can be seen as a thin dark band on the outer surfaces near the functional wear surface **(FW)**. **B**, The outer surface of the tooth fragment (either its anterior or posterior surface) showing that the cementum cover **(C)** surrounded the moiety for much if not all of its length. It is broken away so that a wide expanse of the superficial surface of the enamel **(E)** is exposed. The enamel did not completely surround the moiety, but instead thinned to a sharp edge, forming an enamel dentine junction **(E/D)**. Dentine **(D)** is also visible where the enamel is broken away along the side with the convex curvature.

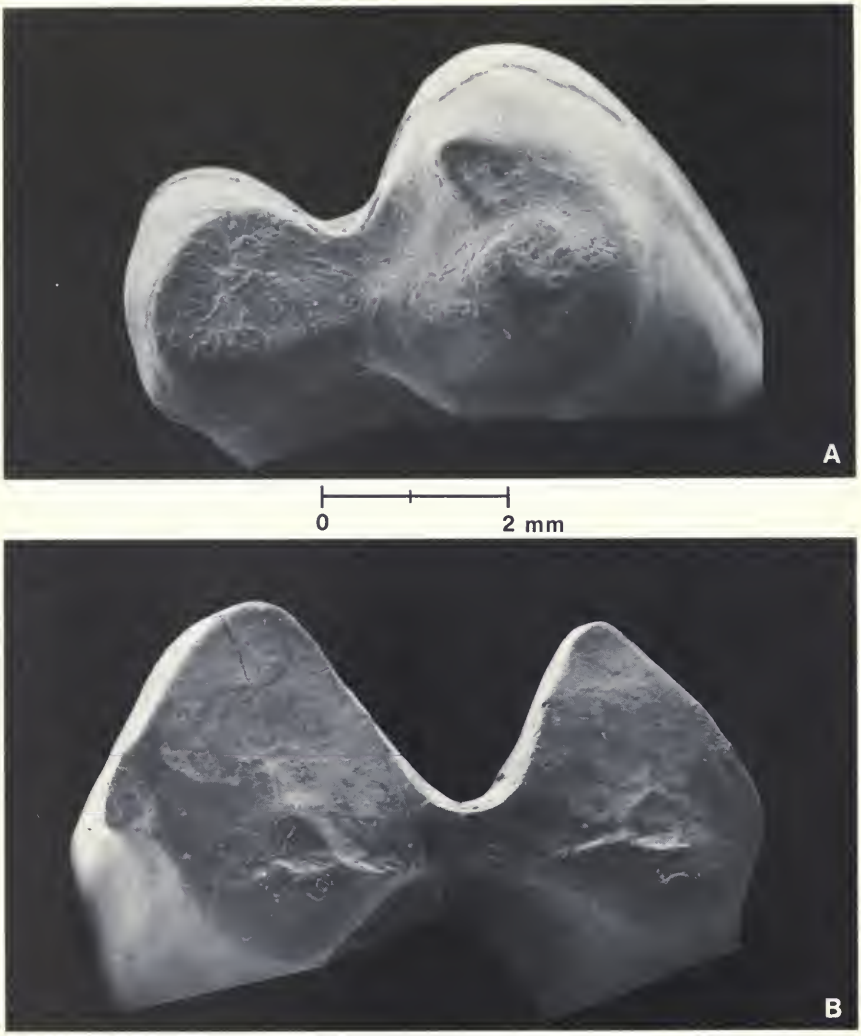


PLATE I. *Lasiorhinus* c.f. *latifrons*. Scanning electron microscope (SEM) photographs of two specimens: **A**, TMM 41106-52, a montage of two exposures showing the occlusal surface of a right M^1 at a young age/wear stage. **B**, WAM 75.1.142, the same for another molar tooth whose position is uncertain.

underlying dentine surface can be seen. There is a ridge that runs transversely across the larger of the two lobes to connect two faint cusps. The smaller lobe has a truncated occlusal surface—a flat facet.

In addition to the wombat materials that have been assigned to *L. latifrons*, an equal number of specimens are indeterminate. These are teeth or scraps that are probably also *L. latifrons*, but there is no good evidence upon which to base an assignment. They are listed below and will be discussed with the assigned specimens. Three of them are from juvenile individuals and preserve some crown features (pl. II).

PLATE II. *Lasiorhinus* gen. and sp. indet. SEM photographs of the occlusal surface of isolated teeth, each at an early age wear stage. **A,** PM 36831, tooth row position uncertain. **B,** PM 36839, probably an M^1, montage of two SEM photos. **C,** WAM 75.1.143, tooth row position uncertain, montage of two SEM photos.

Discussion

Lasiorhinus was a member of the fauna of the region continuously between about 38,000 y B.P. and 7,500 y B.P., although it is absent today. None of the levels indicate any great abundance, but Unit 2 contains appreciably more specimens than any other unit; Units 1, 4–5, and 7 have each produced only a single specimen. The presence of *Lasiorhinus* is not surprising; it lives today on the eastern side of the Nullarbor Plain (east of Eucla).

Vombatidae

Genus and species indeterminate

Material

Trench 2, top 1 ft (= Unit 1, probably Levels 1 or 2)
PM 4781, left M_2 or M_3

Trench 3, Unit 2, Level 1
TMM 41106-114, left M^1 from a subadult individual
TMM 41106-115, molar

Trench 3, Unit 2, Level 2
PM 36831, molar at a very early age/wear stage (pl. II-A)

Trench 4, Unit 2, Level 1
TMM 41106-5024, fragment of a right I^1

Trench 4, Unit 2, Level 2
PM 36837, half molar (fig. 6)
PM 36839, very early age stage molar, probably a LM^1 (pl. II-B)
WAM 75.1.144, half of a lobe of a molar
TMM 41106-5025, one lobe of a molar

Trench 4, Unit 7, Level 2
TMM 41106-5026, one lobe of a molar

Trench 5, Unit 6
WAM 75.1.143, nearly complete molar at very early age stage (pl. II-C)
PM 36840, molar fragment

Several of these indeterminate specimens deserve brief comments:

The extremely early tooth stages represented by PM 36831, PM 36839, and WAM 75.1.143 are of particular interest because they show traces of the original crown structure, which are illustrated (pl. II) by scanning electron micrographs (SEM). PM 4781 and TMM 41106-114 and TMM 41106-115 are at subadult age stages, judging by their sizes, proportions, and wear. They represent some of the older individuals in the collection. One specimen, PM 36832, is eroded in a peculiar manner. Much of its surface may have been removed by chemical leaching. PM 36837 is a longitudinally broken tooth, the broken surface of which has been ground and polished to show the nature of the dentine-pulp cavity and the enamel-cementum and dentine-cementum relationships (fig. 6).

Family PHASCOLARCTIDAE

Phascolarctos Blainville, 1816

Phascolarctos cinereus (Goldfuss, 1817)

Material

Trench 4, Unit 2, Level 2
TMM 41106-628, right M^1 (pl. III-A)
TMM 41106-17, right M^2 (fig. 7A, B)
PM 36815, very worn left M_4 (fig. 7C, D)

This is the second record of this taxon from the Nullarbor Plain; the other record is also from Madura Cave (Milham & Thompson, 1976). That specimen came from the south passage and is apparently reworked from an earlier deposit than the unit in which it was found.

Description

The M^1 is similar to the M^1 of Recent specimens from New South Wales (FMNH 81524) and Victoria (TMM M2946 and FMNH 112541) but differs in size. The Madura Cave specimen is smaller than each of the Recent specimens (table 1). It is at a nearly unworn stage, hence all crests, ridges, and crenulations are strong, but they do not appear to be any more developed than those on the Recent specimens.

The right M^2 shows the same differences from the Recent materials as does the M^1. It too is smaller than the Recent specimens. Length measures of the M^2s of the three Recent specimens available for comparison are shorter than the anterior width measures, whereas the M^3 lengths are greater than the anterior widths (table 1). In the Madura Cave specimen this ratio is 0.92, which is even lower than in any of the Recent M^2s and is far from the proportions seen for the M^3s. On this evidence, it is considered to be an M^2 rather than an M^3. One other

Table 1. Measurements (in mm) and ratios of upper dentitions of fossil and Recent specimens of *Phascolarctos cinereus*.

	Recent			Madura Cave	
Variate	TMM M-2946	FMNH 81524	FMNH 112541	TMM 41106-625	TMM 41106-17
M^1 L	7.9	7.9	7.9	7.0	. . .
AW	8.2	7.6	7.9	7.2	. . .
PW	7.7	7.3	7.0	6.6	. . .
M^2 L	8.1	7.4	7.9	. . .	6.8
AW	8.3	7.5	8.1	. . .	7.4
PW	7.4	6.8	6.7	. . .	6.4
L/AW	0.976	0.987	0.976	. . .	0.92
M^3 L	7.9	7.4	7.5	. . .	. . .
AW	7.8	7.4	7.4	. . .	. . .
PW	6.7	6.2	6.4	. . .	. . .
L/AW	1.012	1.0	1.14	. . .	. . .
M^4 L	7.2	>7.0	7.1	. . .	. . .
AW	6.9	6.9	5.8	. . .	. . .
PW	5.4	5.6	>4.7	. . .	. . .

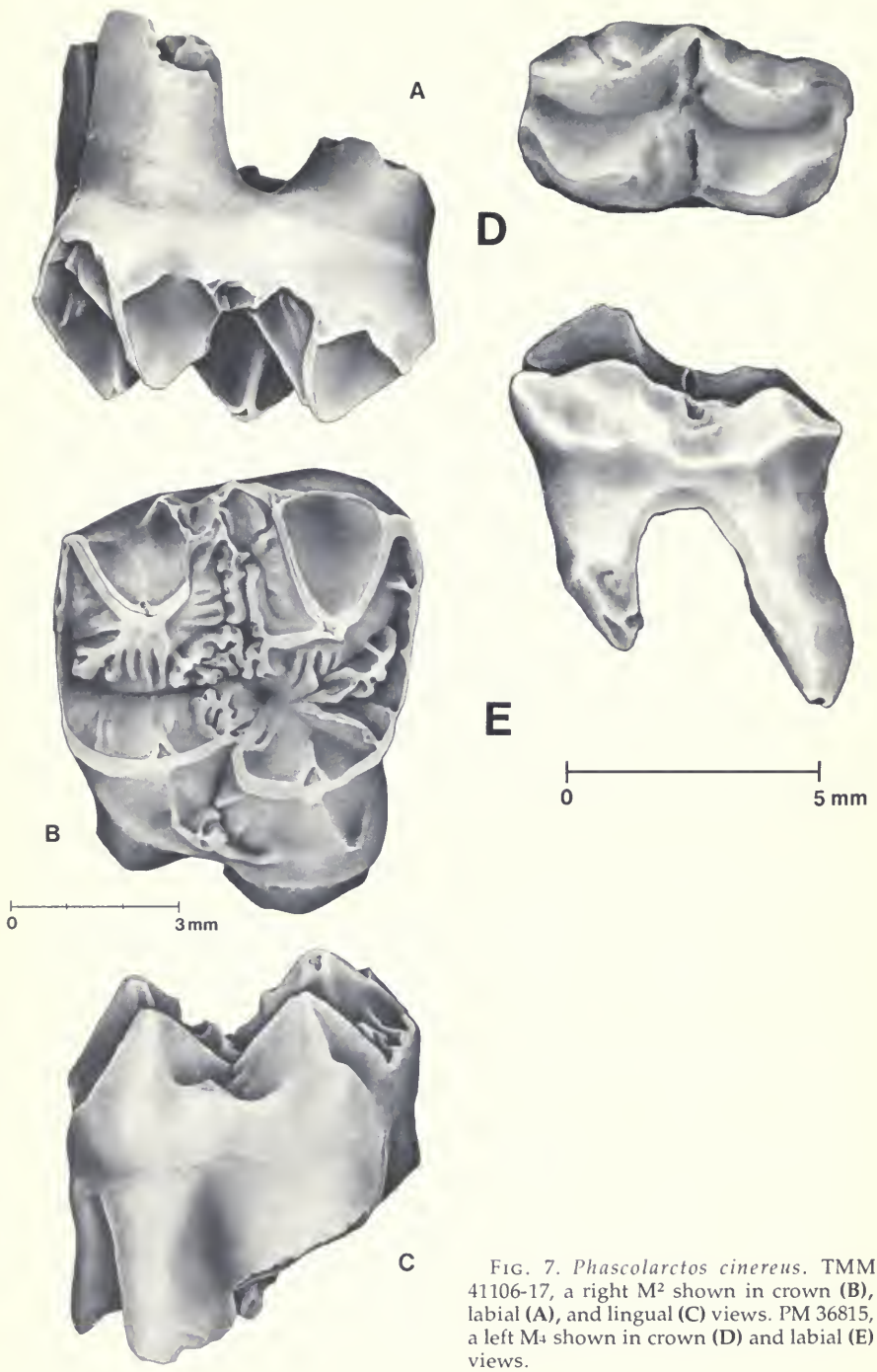


FIG. 7. *Phascolarctos cinereus*. TMM 41106-17, a right M^2 shown in crown **(B)**, labial **(A)**, and lingual **(C)** views. PM 36815, a left M_4 shown in crown **(D)** and labial **(E)** views.

TABLE 2. Measurements (in mm) of lower dentitions of fossil and Recent specimens of *Phascolarctos cinereus*.

	Recent			Fossil	
Variate	TMM M-2946	FMNH 81524	FMNH 112542	Labyrinth Cave cast WAM 69.4.1	Madura Cave PM 36815
M_1 L	7.8	7.6	8.2	8.5	. . .
AW	5.0	4.6	4.8	5.6	. . .
PW	5.3	5.2	5.3	6.0	. . .
M_2 L	8.0	7.5	7.7	8.5	. . .
AW	5.4	4.8	5.2	5.5	. . .
PW	5.3	4.8	5.2	5.8	. . .
M_3 L	8.2	7.5	7.9	8.2	. . .
AW	5.3+	4.9	5.2	5.3	. . .
PW	5.2	4.8	5.2	5.3	. . .
M_4 L	8.1	7.5	8.0	8.2	6.4
AW	5.1	4.8	5.4	5.0	>3.8
PW	4.5	4.5	4.8	5.0	>3.4

minor difference can be seen; the tooth has a nearly straight anterior edge compared with the Recent specimens in which it bulges forward slightly.

The M_4 is badly etched, with most of its enamel surface destroyed. Wear had breached the tips of the major cusps and crests to expose dentine. The protoconid and hypoconid are deeply worn on their tops, and the enamel on the labial side of the whole tooth is gone. The exposed dentine of the labial side is polished, which could have resulted from either masticatory wear or postdepositional leaching. The tooth appears to be very elongate and narrow (table 2), but the appearance is exaggerated by the loss of the labial enamel surface and a similar but less extreme loss of enamel on the lingual side. The crenulations of the original enamel surface can be vaguely seen in the central valley. The posterior sides of hypoconid and entoconid and the entire postcingulum are beveled by wear as is typical of worn M_4s in the living form. The metaconid and entoconid are higher and thinner and have better developed longitudinal crests than the labial cusps, as in the Recent comparative specimens and a fossil from Labyrinth Cave (Merrilees, 1969, WAM 69.4.1). The labial cusps, with their associated crests, form open selenes of about equal proportions as in the living form. The roots, especially the posterior, are inclined posteriorly, and both are eroded and polished.

DISCUSSION

The Madura Cave material is slightly smaller than the three modern specimens of *Phascolarctos cinereus* we have for comparison (tables 1, 2). It is also slightly smaller than the modern sample reported by Bartholomai (1968) and the Pleistocene examples from Mammoth Cave (Glauert, 1910).

Phascolarctos stirtoni from the Cement Mills limestone of southeastern Queensland differs from *P. cinereus* in being 25% to 30% larger and in some minor and variable dental characters (Bartholomai, 1968). Marshall (1973a) reports the presence of *Phascolarctos* remains referable to *P. stirtoni* from Pleistocene cave deposits at Narracoorte, South Australia.

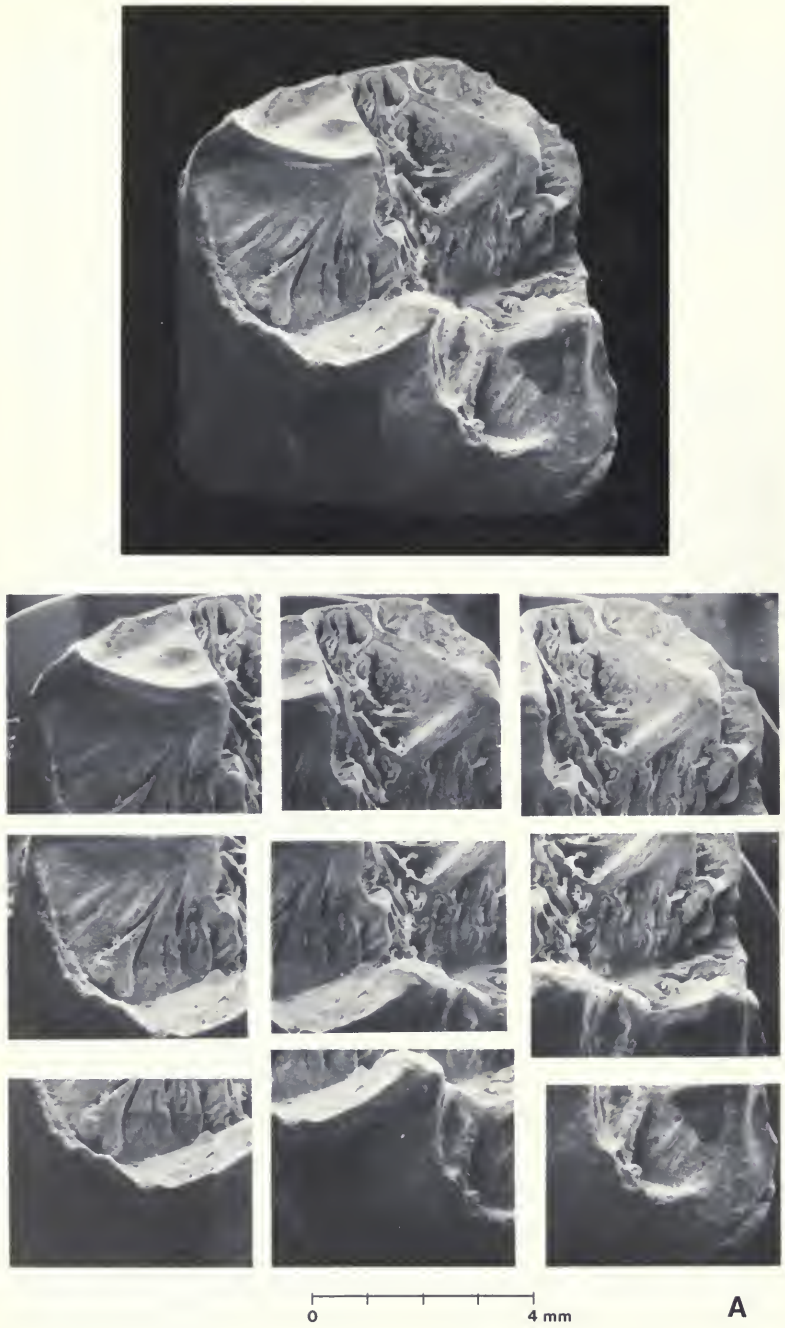


PLATE III. SEM photo montages of: **A,** *Phascolarctos cinereus,* TMM 41106-628, a right M^1 in posterolingually oblique view of occlusal surface. **Top:** Montage of all ten exposures. **Bottom:** Nine separate individual exposures are shown.

PLATE III. SEM photos of: **B,** *Trichosurus vulpecula,* PM 36830, a left M_1 in posterodorsal oblique view; **C,** *Pseudocheirus peregrinus,* TMM 41106-5027, stereopair of a right M^1 in crown view (rotate 90° for stereo viewing).

The Madura Cave *Phascolarctos* is referable to *P. cinereus* on the basis of all characters of the material currently available. A larger sample would be necessary to determine whether the apparent small size is significant.

Phascolarctos cinereus is found today in sclerophyll forest from Queensland to Victoria east of the Great Dividing Range (Marlow, 1958). According to Tyndale-Biscoe & Calaby (1975), its optimum habitat is tall open forest, but some of its range is in dry woodland, which implies that dense forest is not a prerequisite for its existence (Calaby, 1971, p. 87). Its presence in Pleistocene deposits of the Nullarbor Plain indicates somewhat moister conditions during the Pleistocene but not necessarily those of its optimum habitat.

Phascolarctos cinereus is known from late Pleistocene deposits at Lake Menindee and Lake Victoria, southwestern New South Wales (Tedford, 1967; Marshall, 1973b), and from Holocene deposits in McEachern's Cave, southwestern Victoria (Wakefield, 1967). Madura Cave is almost exactly halfway between the Pleistocene localities in eastern Australia and those of southwestern Australia (Glauert, 1910; Merrilees, 1969; Archer, 1972). The age of the Madura Cave material (20,000 ± 430 y B.P.) supports the hypothesis put forth by many people (Serventy, 1951, 1953; Main et al., 1958; Gentilli, 1961) that faunal exchange between east and west took place across this area during the last glacial maximum.

Family PHALANGERIDAE

This family is represented by two teeth, one each of *Trichosurus vulpecula* and *Pseudocheirus peregrinus*.

Trichosurus Lesson, 1828

Trichosurus vulpecula (Kerr), 1792

Material

Trench 4, Unit 2, Level 2
PM 36830, left M_1 (fig. 8, pl. III-B)

Description

This tooth compares well with the available modern examples of *T. vulpecula* cf. *hypoleucas* from southwestern Australia, but it is slightly smaller. It is from a juvenile because it is virtually unworn; a comparably worn modern example has functional dP_4s. Its trigonid is narrower than the talonid, and the protoconid stands higher than any other cusp. In crown view the protoconid is centrally located within the trigonid and is connected to a distinct metaconid that lies at the lingual edge of the crown. The metaconid stands nearly as high as the protoconid and entoconid, which are the highest cusps. There is no distinct paraconid: the anterior crest from the protoconid extends nearly straight forward to the rounded anterior point of the tooth. There are weak but distinct anterolabial and anterolingual cingula. The posterior cingulum is small. It swings down from high on the entoconid and is tied to a lower, stout hypoconid immediately labiad of the bottom of the "V" of the crest between hypoconid and entoconid. Although all of the available Recent Western Australian comparative specimens show considerable variation among themselves in

FIG. 8. *Trichosurus vulpecula*, PM 36830, a left M_1 shown in crown **(A)** and labial **(B)** views.

TABLE 3. Measurements (in mm) of *Trichosurus*, M_1.

Specimen No. and taxon	N	L Range	L Mean	AW Range	AW Mean	PW Range	PW Mean
Madura Cave							
PM 36830, *T. vulpecula*	1	. . .	4.40	. . .	3.00	. . .	3.25
Holocene and Recent, S.W. Australia							
TMM M-849, M-1743, M-2031a-c, M-2032; TMM 40238-1, 41110-6 through 10, *T. v. hypoleuca*	12	4.70–5.30	5.12	2.75–3.30	3.02	3.25–3.80	3.53
Recent							
FMNH 98783, *T. v. vulpecula*	1	. . .	5.30	. . .	3.15	. . .	3.35
FMNH 60936, *T. v. johnstonii*	1	. . .	5.30	. . .	2.90	. . .	3.45
USNM 221121, *T. caninus*	1	. . .	5.45	. . .	3.10	. . .	3.70

the stoutness of the cingulum and its connecting ridges, they have a more poorly developed posterior cingulum complex than is seen in the eastern forms (*T. v. vulpecula*, *T. v. johnstoni*, or *T. caninus*). In these the posterior cingulum is strongly developed. The Madura Cave specimen is somewhat smaller than Recent specimens from southwestern and southeastern Australia (table 3), although we have not had adequate samples from the latter area. It is most like the Recent specimens from southwestern Australia referred to *T. v. hypoleucas*. Comparative material of *T. v. ruficollis* was not available.

Pseudocheirus Ogilby, 1837

Pseudocheirus peregrinus (Boddaert), 1785

MATERIAL

Trench 3, Unit 2, Level ? (probably Level 1)
TMM 41106-5027, right M^1 (fig. 9, pl. III-C)

DESCRIPTION

The protocone, paracone, metacone, and hypocone of the Madura Cave specimen each has a simple crescentic form with no secondary ridges. The paraconule and metaconule are asymmetric. The long arm of the paraconule extends posteriorly into the central basin; the long arm of the metaconule extends into the "V" formed by the junction of the posterior crest of the paracone and the anterior crest of the metacone. The enamel of the tooth is smooth. There are small secondary ridges from the hypocone and posterior crest of the protocone. All of these characteristics are found in *P. peregrinus*, and the Madura Cave specimen is thus referred to that species. Dental measurements of the M^1 from Madura Cave and of some fossil and Recent comparative materials are given in Table 4.

DISCUSSION

Pseudocheirus peregrinus and *Trichosurus vulpecula* both have disjunct populations in southwestern Australia and in eastern Australia today. Both have been

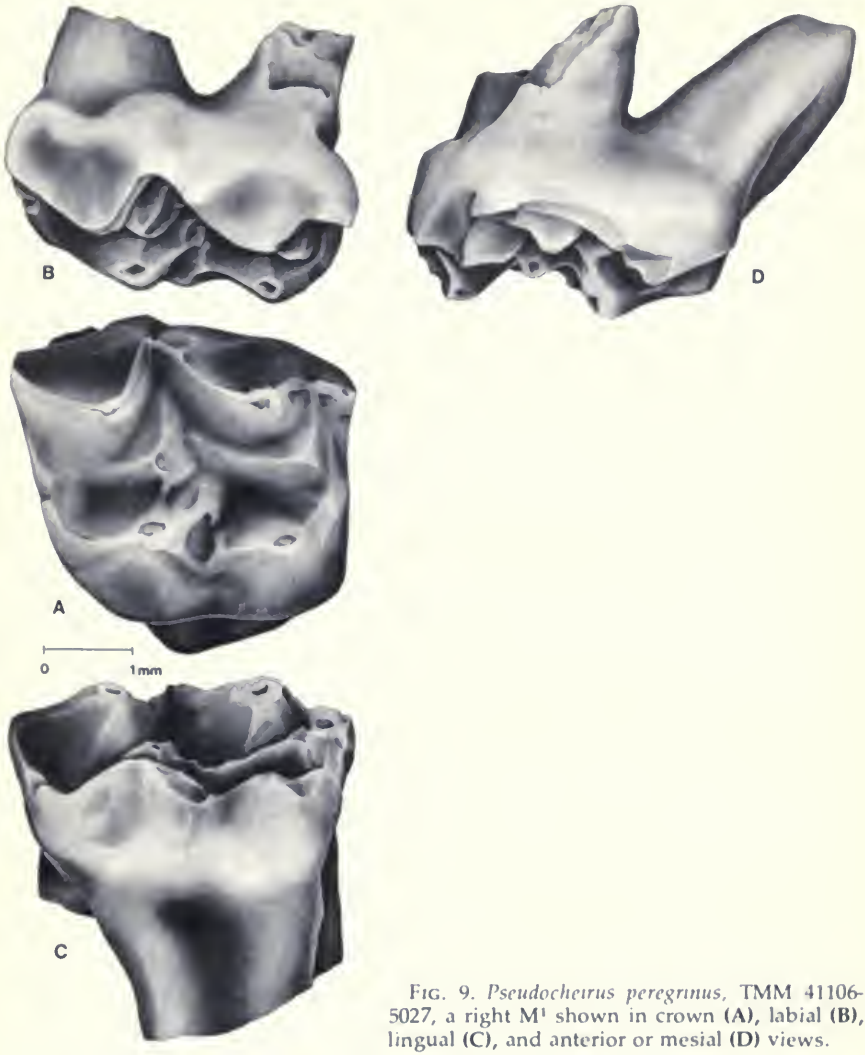


FIG. 9. *Pseudocheirus peregrinus*, TMM 41106-5027, a right M^1 shown in crown **(A)**, labial **(B)**, lingual **(C)**, and anterior or mesial **(D)** views.

TABLE 4. Measurements (in mm) on fossil and Recent specimens of *Pseudocheirus peregrinus* and *P. convolutor*.

Specimen No.	Tooth	L	AW	PW
Madura Cave				
TMM 41106-5027	M^1	4.00	3.10	3.30
Pleistocene, S.W. Australia				
TMM 41237-2	M^1	4.70	3.60	4.00
TMM 41110-2	M^1	4.70	3.70	4.00
Recent				
FMNH 98771	M^1	4.30	3.50	3.90
	M^2	3.80	3.10	. . .
	M^3	3.90	2.90	. . .

found in surficial deposits in other Nullarbor caves: from Webb's Cave (Lundelius 1957, 1964) and Murraelellevan Cave (Lundelius & Turnbull, unpublished data) and *T. vulpecula* from Cave N41 of Anderson (1964) and Weebubbie Cave (Lundelius & Turnbull, unpublished data). *Trichosurus vulpecula* has been reported from Horseshoe Cave (Archer, 1974), but without stratigraphic context. As in the case of *Cercartetus concinnus*, these occurrences do not necessarily indicate present or recent historic occupancy of this region. They probably indicate their presence on some parts of the Nullarbor Plain after the time of their latest known record in the Madura Cave sequence (15,600 y B.P.) to judge by the C^{14} date of 3,300 y B.P. on a mummy of a thylacine from Murraelellevan Cave (see discussion of *Cercartetus concinnus*). The occurrence of these taxa in Unit 2 with other taxa characteristic of more mesic conditions than the present is consistent with their known distributions and habitat requirements.

Family BURRAMYIDAE

Cercartetus Gloger, 1841

Cercaërtus Burmeister, 1837.
Cercartus Gloger, 1841.
Dromicia Grey, 1841. Grey's Australian Appendix, vol. ii, p. 407.
Eudromicia Mjoberg, 1916.
Cercartetus Iredale & Troughton, 1934. A checklist of the mammals recorded from Australia. Mem. Austral. Mus., 6:122.
Cercartetus Wakefield, 1963. The Australian pigmy-possums. Victoria National, 80(4):99–116.

Cercartetus concinnus (Gould), 1845

Dromicia concinna Gould, 1845. Proc. Zool. Soc., 1845, p. 2.
Phalangista (D) *concinna* Waterhouse, 1846. Nat. Hist. Mus. U.I., p. 314.
Phalangista (D) *neilli* Waterhouse, 1846. Nat. Hist. Mus. U.I., p. 315.
Dromicia concinna Thomas, 1888. Cat. Marsup. Brit. Mus., p. 146.

Material

Trench 3, Unit 2, Level ?
WAM 75.1.137, right ramus with alveoli for all teeth (fig. 10B)

Trench 4, Unit 2, Level 2
PM 36817, edentulous left ramus with alveoli of I_1, molars, and most of intervening teeth (fig. 10A)
PM 36818, edentulous left ramus with alveoli for all teeth (fig. 10B)
TMM 41106-5006, edentulous right ramus with alveoli for incisors and M_3.
PM 36819, edentulous left ramus fragment with alveoli for I_1 through M_2 (fig. 10A)
TMM 41106-5007, edentulous right ramus with alveoli for P_4 through M_3 (fig. 10B)

Trench 4, Units 4–5
TMM 41106-3, edentulous right ramus with alveoli for all teeth (fig. 10B)
TMM 41106-5001, right ramus with M_1 and alveoli for I_1, and I_3, P_{3-4}, M_2 (fig. 10B; pl. IV-D)
TMM 41106-5002, edentulous left ramus with alveoli for I_1–M_2 (fig. 10A)

TMM 41106-5003, left I_1 (pl. IV-H)
TMM 41106-5004, right M^1 (pl. IV-A)
TMM 41106-5005, right M^2 (pl. IV-B)
TMM 41106-5008, edentulous right ramus with alveoli for all teeth (fig. 10B)
PM 36823, left M_1 (pl. IV-E)
PM 36824, right M_1 (pl. IV-F)
WAM 75.1.139, left M_1 (pl. IV-G)
PM 36826, left I_1 (pl. IV-I)
PM 36820, edentulous left ramus fragment with alveoli for all teeth (fig. 10A)
PM 36821, edentulous left ramus with alveoli for all teeth (fig. 10A)

Trench 4, Unit 7, Level 2
PM 36827, right M^2 (pl. IV-C)

Trench 5, Unit 4?
WAM 75.1.138, edentulous left ramus with alveoli for all teeth (fig. 10A)
TMM 41106-5009, edentulous right ramus with alveoli for I_1 and M_{1-3}
TMM 41106-5010, edentulous right ramus with alveoli for all teeth (fig. 10B)
PM 36822, edentulous left ramus with alveoli for all teeth (fig. 10A)

Comparative materials:

FMNH 34721	*Cercartetus concinnus* from Tambellup, Western Australia
TMM M 842	*Cercartetus concinnus* from Kybybolite, Western Australia
TMM M 831	*Cercartetus concinnus* from near Bridgetown, Western Australia
TMM M 832	*Cercartetus concinnus* from near Bridgetown, Western Australia
Monash 977	*Cercartetus concinnus* locality unknown

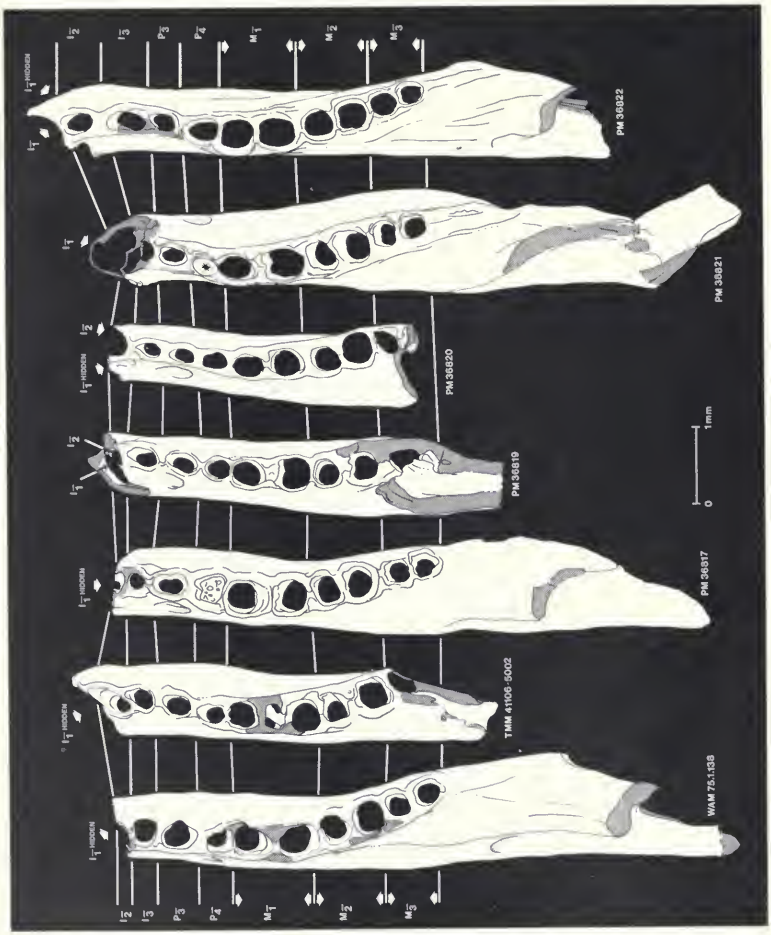
and casts of:

AMNH 119720	*Cercartetus concinnus* from Margaret River area, Western Australia
AMNH 119723	*Cercartetus concinnus* from Picton Junction, Western Australia
AMNH 191027	*Cercartetus caudata* from Mt. Otto, New Guinea
AMNH 191006	*Cercartetus caudata* from Mt. Wilhelm, New Guinea

Comparisons of fossil and Recent *C. concinnus* with *C. nanus, C. lepidus, C. caudatus* were made by reference to Turnbull & Schram (1973). The four species of *Cercartetus* (*sensu* Wakefield, 1963) show that *C. nanus* and *C. concinna* both have only three molars, whereas *C. lepidus* and *C. caudatus* have the usual marsupial complement of four. Between *C. nanus* and *C. concinnus* there is a marked size difference in the P_4: in the former, P_4 is double rooted and is several times larger than that of *C. concinnus*. The Madura Cave sample conforms to *C. concinnus*; the differences noted below between the fossils and the Recent specimens are considered to be intraspecific.

Description

The 16 ramus fragments have the same basic form but show minor variations (fig. 10). They indicate the normal lower tooth formula for *Cercartetus concinnus* of I_{1-3}, P_{3-4}, M_{1-3}. No P_4s were recovered, but some variation is indicated by


WAM 75.1.138
TMM 41106-5002
PM 36817
PM 36819
PM 36820
PM 36821
PM 36822
0
1mm

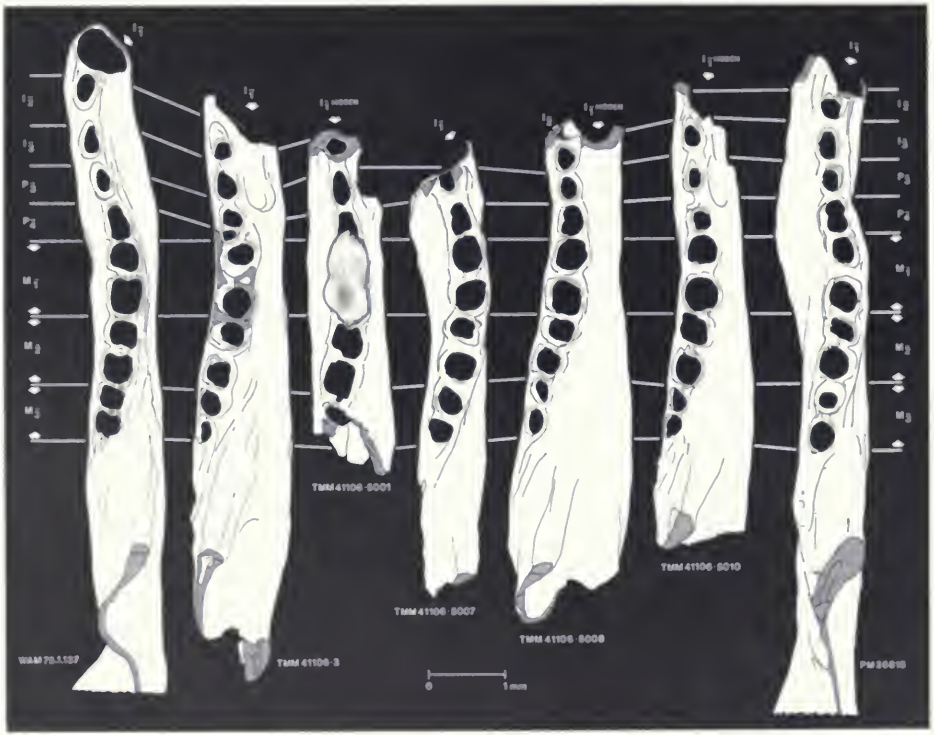


FIG. 10. *Cercartetus concinnus*. Schematic outlines of 14 ramus fragments; all are edentulous but one. Certain alveoli are identified to assist in comparisons and to demonstrate the kind of variation among them. **Above,** Seven left rami are as follows (left to right): WAM 75.1.138; TMM 41106-5002; PM 36817; PM 36819; PM 36820; PM 36821; PM 36822. **Below,** Seven right rami are as follows (left to right): WAM 75.1.137; TMM 41106-3, TMM 41106-5001; TMM 41106-5007; TMM 41106-5008; TMM 41106-5010; PM 36818. Isolated teeth of this taxon are illustrated in Plate IV.

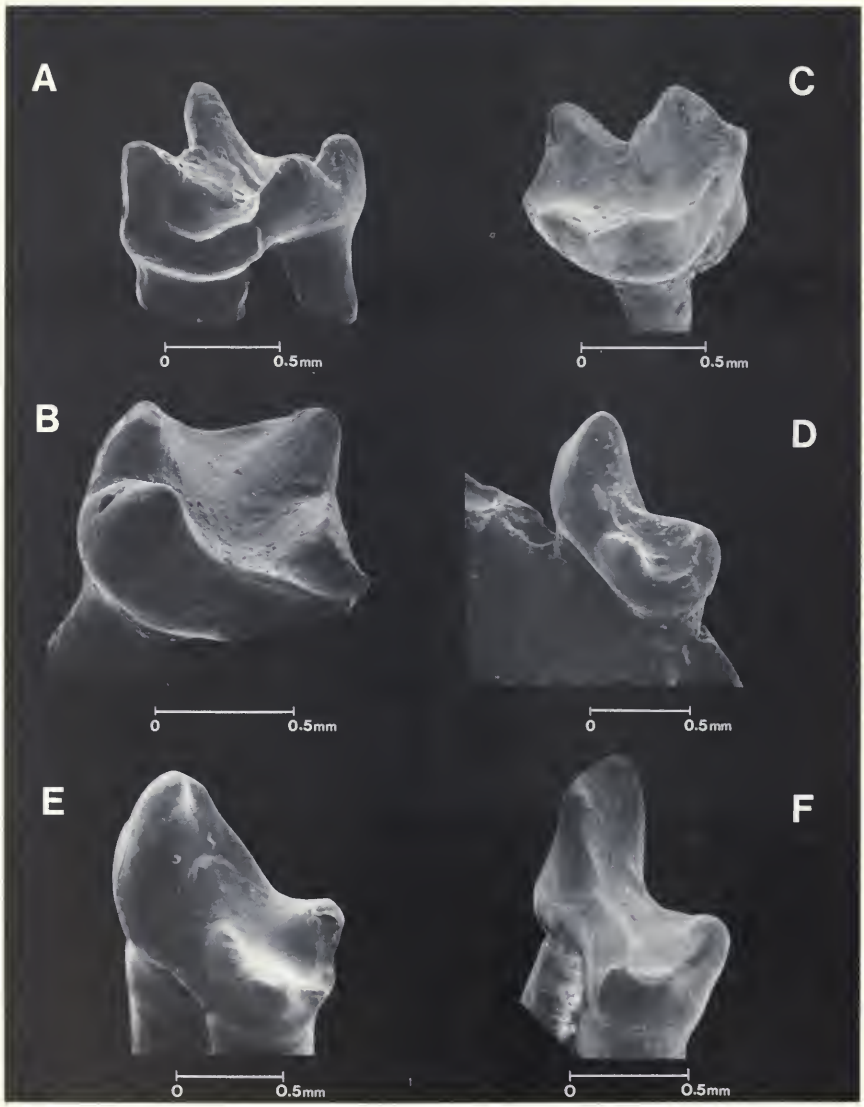


PLATE IV. *Cercartetus concinnus*. SEM photos of six of the nine teeth representing this taxon from Madura Cave: **A**, TMM 41106-5004, right M^1; **B**, TMM 41106-5005, right M^2; **C**, PM 36827, right M^2; **D**, TMM 41106-5001, right M_1 in ramus fragment; **E**, PM 36823, left M_1; **F**, PM 36824, right M_1.

PLATE IV. *Cercartetus concinnus*. SEM photos of three of the nine teeth representing this taxon from Madura Cave: **G**, WAM 75.1.139, left M_1; **H**, TMM 41106-5003, left I_1 shown in several views; **I**, PM 36826, left I_1 shown in several views.

differences in size and form of alveoli for it, which may be very small and single (as in TMM 41106-3 and TMM 41106-5010), large and single but with a weak constriction (as in TMM 41106-5001, PM 36817, PM 36821, WAM 75.1.138, and WAM 75.1.137), or paired for a small double-rooted tooth (as in TMM 41106-5008 and PM 36818). The major differences between the Madura Cave specimens and the modern comparative materials are the greater depth of the mandible of the fossils, particularly in the region of the premolars and M_1, and the larger size of P_3 and P_4 as indicated by their alveoli. In the modern specimens the teeth are minute (about the size of the point of a pin).

The M^1 (pl. IV-A) is similar to that of the Recent specimens. It is a four-cusped, three-rooted tooth that is elongate anteroposteriorly. The size order of the cusps is paracone > metacone ≥ protocone > hypocone. The paracone and metacone are high, laterally compressed cusps with anteroposterior crests from their apices. These cusps along with their crests and a tiny, laterally compressed parastyle and an even smaller metastyle form an almost straight ectoloph. The protocone and hypocone are lower than the labial cusps and are laterally compressed to a lesser degree than the labial cusps and are located on the lingual edge of the tooth. Both have anterior and posterior crests. A nearly straight anterior cingulum extends from the parastyle to a point immediately anterior to the end of the elongate central valley where a cingular cuspule is located. The cingulum then bends posterolingually and joins the anterior crest of the protocone. At the posterolingual corner there is another cingular cuspule that is more pronounced in the fossil tooth than on any of the Recent specimens. An inconspicuous labial cingulum constitutes the stylar shelf. The anterolabial root supports the paracone, the anterolingual root the protocone, and the posterolabial root the metacone. No root is associated with the hypocone, but the one for the metacone has a lingual expansion and doubtless provides support for both cusps.

The M^2s are four-cusped, three-rooted teeth (pl. IV-B, C). They are elongated, tapered posteriorly, and basined. The cusps in order of decreasing size are paracone > protocone ≥ metacone > hypocone. The four major cusps are located on the perimeter of the tooth. The paracone and metacone are laterally compressed, crested, and stand higher than the lingual cusps. There is a parastyle but no metastyle. The protocone is somewhat crescentic, with its low crests forming the arms of the crescent. The anterior crest extends labially to the parastyle with only a trace of the homologue of the cingular cuspule seen on the M^1. The posterior crest of the metacone curves labially to a posterior lingual corner that is situated almost on the longitudinal axis to the tooth. This point may be the homologue of the posterior cingular cusp of the M^1 because it is in the equivalent position and is joined by the oblique posterior crest of the hypocone. There is a small stylar shelf labial to the paracone and the anterior half of the metacone. This feature is somewhat variable in our comparative specimens.

The I_1s are long, enamel-covered, slightly tapered cylinders that are weakly spatulate for the anterior third of their length (pl. IV-H, I). Ridges extend posteriorly from the tip on the ventromedial and dorsolateral edges. The I_1s of *Cercartetus* are less curved and less spatulate than those of *Acrobates* or *Distochoerus*.

The M_1s (pl. IV-D–G) are similar to those of the modern specimens. Each has

three cusps that make up an anteriorly tapered, elongate crown. The anterior cusp is the protoconid; it is the only trigonid cusp and is the largest and highest cusp of the tooth. It occupies nearly the anterior half of the tooth. It has a somewhat triangular cross section and is crested along its posterolingual side from its tip to the midpoint of the lingual side of the tooth where it joins a short crest from the entoconid in the saddle between the two cusps. The entoconid is smaller than the hypoconid but it stands nearly as high. It has a weak posterior crest that extends toward the minute hypoconulid at the posterolingual corner of the tooth. The hypoconid is V-shaped in crown view. The anterior limb of the "V" is a crest, the cristid obliqua (or premetacristid, l'''b of Hershkovitz, 1971), that extends diagonally anterolingually to the base of the protoconid. The posterior limb swings posterolingually, then lingually to the hypoconulid. There is a little variation in the degree of development of the cusps on our comparative material and more variation in the fossils. On PM 36824 there is a trace of the metaconid near the top of the protoconid on its posterolingual crest. This specimen also has a faint anterior cingulum tied to the anterior crest of the protoconid. In PM 36823 all cusps are less prominent than in two of the other fossil examples, and WAM 75.1.139, which is the smallest tooth of all, has the weakest cusp development. Some of this variation may be due to differences in wear.

Discussion

Cercartetus concinnus is found living today as two disjunct populations, one (*C. c. concinnus*) in southwestern Australia with its eastern limit at Balladonia, and one (*C. c. minor*) in Western Victoria and South Australia with its western limit at Ceduna (Wakefield, 1963). Marlow's map (1962) shows a continuous range across the coastal strip of the Great Australian Bight, but lacks the Victorian and southeastern portion of the South Australian part of the range because Marlow's work preceded the Wakefield report. We assume that the strip along the Bight was an inference on Marlow's part because we can find no firm reports for the area between Ceduna and Balladonia. Further, Wakefield (1963, p. 100) is quite explicit on this point. He states, "The South Australian and Victorian population of the species is geographically isolated from that of Western Australia, and the two groups differ appreciably in morphology."

Although apparently absent from the Nullarbor Plain today, it has been recorded there in deposits in three other caves besides Madura Cave: Murraelellevan Cave (Lundelius, 1957, 1963; Partridge, 1967), Thylacine Hole (Lowry & Merrilees, 1969), and Horseshoe Cave (N59; Archer, 1974). Unfortunately, there are no dates available for the occurrences reported by Lundelius. Although the material from Murraelellevan Cave was collected from the surface, it could be several thousand years old. That this is possible is demonstrated by a C^{14} date of 3,300 y B.P. on a mummified carcass of *Thylacinus* from Murraelellevan Cave (Partridge, 1967) and a C^{14} date of 4,600 y B.P. on another mummified carcass from Thylacine Hole (Lowry & Merrilees, 1969).

Cercartetus concinnus is represented in all of the fossiliferous Pleistocene units of Madura Cave. It is missing from Unit 1, the Holocene unit, and the absence is believed to be real and not just an accident of sampling, because large volumes of that unit were processed. It should be recalled that Unit 1 lies unconformably

upon Unit 2 deposits dated at 15,600 y B.P. in Trench 3 and 18,900 y B.P. in Trench 4. Our only date for Unit 1 was for the top 1 foot at 7,500 y B.P. At face value, this suggests that *Cercartetus* was reasonably abundant during the last 15,000 to 20,000 years of the Pleistocene, was rare or extinct in the area during the early part of the Holocene, and reappeared in the later Holocene, only to die out again sometime between 3,300 y B.P. and historic times.

According to Wakefield (1963), who has marshalled the most evidence about the habitat requirements of *C. c. concinnus*, "The Mundarda is abundant in Jarrah forests (*Eucalyptus marginata*), where there is an undergrowth of sclerophyllous shrubbery containing many of the Myrteaceae and Proteaceae." He describes these regions and states that *C. c. concinnus* also occurs in the Tuart forest (*E. gomphocephala*) in scrubby areas and that it is absent from the Karri forests (*E. diversicolor*) where rainfall exceeds 40 inches per annum. He further points out that in the drier parts of its range (conditions wherein some eucalypts are present to provide homes for *Cercartetus* and heath or mallee, with their abundant Myrteaceae and Proteaceae and other nectar producers, provide food) the environment is still adequate. Possibly, the increase in mallee scrub cover 4,000 to 6,000 y B.P. that was reported for Norina and Madura by Martin (1973) on the basis of pollen studies could have provided the minimum habitat base for the repopulation by *Cercartetus* for a time in the late Holocene. Subsequent to this peak in the ratios of Myrteaceae/chenopod-type pollens, the ratios are shown to drop, and Martin reports that from the period 4,000 to 5,000 y B.P. to the present the scrub cover has declined markedly. This history of change of the vegetation is consistent with the history of *Cercartetus* in this region in the light of its habitat requirements.

SUMMARY

The families Phascolarctidae, Phalangeridae, and Burramyidae are represented in the Madura Cave deposits by relatively little material. All are from the Pleistocene units. The family Vombatidae is represented in both Pleistocene and Holocene units. All except *Phascolarctos* are known from Holocene deposits in other caves of the Nullarbor Plains, but only *Lasiorhinus latifrons* is extant in this area. The presence of *Phascolarctos* in the Pleistocene deposits indicates that the time of the last major interchange between the more humid areas of southwestern and southeastern Australia was during the last glacial maximum. The presence of *Trichosurus*, *Pseudocheirus*, and *Cercartetus* in Holocene deposits in other cave deposits in this area indicates continued post-Pleistocene increase in aridity. The evidence for climatic change presented by these taxa appears to be consistent with that suggested by the Dasyuridae and Peramelidae in prior reports (Lundelius & Turnbull, 1973, 1975, 1978, 1981).

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